Contents lists available at ScienceDirect

Fisheries Research

Diet analysis of Atlantic salmon (*Salmo salar*) post-smolts after the ecological regime shift in the Northeast Atlantic

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ARTICLE INFO

ABSTRACT

Transition from freshwater to saltwater presents multiple challenges for anadromous Atlantic salmon, and survival during this critical life-stage is thought to influence adult population abundance. Despite this, the role of feeding, which influences growth and therefore survival, is poorly studied. Here, we analyzed the diet of 580 post-smolts captured in four Norwegian fjords in 2018 and 2019. Post-smolt diet mainly consisted of fish larvae (Teleostei), krill (Euphasiidae), planktonic amphipods, and insects. However, diet varied among fjords and years. For example, post-smolts in Altafjord in northern Norway displayed a higher frequency of fish larvae in their diet compared to post-smolts from fjords in western Norway, although this effect was less clear in 2019 than in 2018. Post-smolts consuming fish larvae and/or krill displayed substantially higher feeding ratios, and these fish were on average 0.52 cm longer. This observation underpins results from earlier studies suggesting that consumption of fish larvae is important for marine growth and ultimately survival. The dietary observations reported here may therefore have implications for spatial and temporal patterns in Atlantic salmon marine survival rates in this region. Furthermore, we did not detect any clear differences in diet between post-smolts analyzed here in comparison with post-smolts collected in the same region approximately 20 years earlier. As there has been a well-documented ecological regime shift in the Northeast Atlantic between the present and earlier studies, we conclude that it has not had a large impact on post-smolt feeding conditions within Norwegian fjords.

1. Introduction

During the past few decades, many wild Atlantic salmon populations have dramatically declined (ICES, 2021; Parrish et al., 1998). Mortality, especially during the early post-smolt stage (life stage from entering the marine environment for the first time and the following months) of this marine migration is high (Hvidsten and Møkkelgjerd, 1987; Thorstad et al., 2012), and probably plays a major role in regulating adult population abundance (Friedland et al., 2000). During this early migratory phase, post-smolts face a variety of predators, must adjust to different food sources, undergo physiological changes in response to the transition from freshwater to the marine environment, and are exposed to new pathogens. In general, marine survival rates of salmon are correlated with growth within the first weeks at sea (Hvidsten et al., 2009; Thorstad et al., 2012). Additionally, post-smolts have to deal with the tradeoff between energy acquisition to ensure growth while minimizing the risk of predation (Post and Parkinson, 2001). Acquisition of food is crucial as it not only provides energy to support basal metabolism, but also for somatic growth (Amundsen and Sánchez-Hernández, 2019). Post-smolts

must therefore time their migration with regards to availability of prey of appropriate size and abundance (McCormick et al., 1998; Thorstad et al., 2012). Rapid growth achieved through feeding (Brodeur and Pearcy, 1987), feeding behavior, but also food availability and quality, are thus key factors in post-smolt survival (Levings et al., 1994; Salminen et al., 2001; Hvidsten et al., 2009). Feeding behavior and other factors influencing mortality in different life stages (such as predation or competition) are difficult to measure or observe directly (Amundsen and Sánchez-Hernández, 2019). Therefore, analyzing stomach contents can provide useful data on trophic interactions, energetic status of the fish and their feeding strategies.

The diet of salmon varies between the different life stages. To date, knowledge about the diet and feeding strategies of salmon post-smolts in the sea is limited. From dietary studies conducted in the marine environment (Levings et al., 1994; Andreassen et al., 2001; Rikardsen et al., 2004; Haugland et al., 2006; Hvidsten et al., 2009; Aykanat et al., 2020; Utne et al., 2021), we know that salmon appear as opportunistic, strictly carnivorous feeders with a diet consisting mainly of fish and fish larvae, euphausiid species and planktonic crustaceans. The dietary composition

and feeding intensity of post-smolts while migrating through the coastal zone may also vary with latitude, as higher feeding ratios and higher percentage of fish in the diet of salmon post-smolts from northern Norway, in comparison with post-smolts from southern Norway, have been reported (Rikardsen et al., 2004). From studies including a time-series, it is also known that besides spatial differences, diet also varies between years (Rikardsen et al., 2004; Haugland et al., 2006; Utne et al., 2021). An ecological regime shift occurred in the Northeast Atlantic around year 2004, with a reduction of Arctic water masses transported into the Norwegian Sea leading to reduced productivity in the region (Skagseth et al., 2022). Post-smolts feeding in the Norwegian Sea after the regime shift displayed reduced stomach fullness (Utne et al., 2022), and adults returning to Norwegian rivers had lower growth and later age at maturation due to the large ecological changes in the sea (Harvey et al., 2022; Vollset et al., 2022). Whether the observed regime shift also impact the coastal ecosystems, thereby affecting prey availability for post-smolts in fjords and coastal areas, is still unknown.

The marine phase of the salmon's life cycle, and specifically, the early phase where post-smolts in some areas migrate through long fjords before they reach the open coast, represents a critical window of mortality vs. survival, ultimately impacting population abundance. Feeding opportunities during this stage of the life cycle, and variations in prey abundance in time and space, are likely to be important in regulating survival. Despite this, little is known about the temporal and spatial feeding patterns of post-smolts migrating through fjords and coastal areas. Therefore, and to provide data on this knowledge gap, we studied the diet of salmon post-smolts captured by trawling from four Norwegian fjords over two years. The main objectives were to examine the diet, how this varied geographically and temporally, whether stomach fullness was correlated to feeding on specific prey groups, and finally, whether post-smolt body length and condition factor were correlated with diet. While earlier diet studies from Norwegian fjords have presented data prior to the ecological regime shift in the Northeast Atlantic, the data presented in this study are collected afterwards. The results are therefore discussed in relation to results from earlier studies in the same regions in order to identify whether there have been any long-term shifts in post-smolt feeding.

2. Materials and methods

2.1. Study area and sampling

Post-smolts captured by trawling in 4 different fjords in Norway were analyzed (Fig. 1): Altafjord (70°N), Sognefjord (61°N), Hardangerfjord (60°N) and Boknafjord (59°N). Fish were captured in two separate years (2018 and 2019) under the NALO program. NALO is an annually conducted survey where post-smolts in Norwegian fjords are sampled to monitor sea lice infestation of wild salmonid fish (Myksvoll et al., 2018). Each fjord was trawled for a period of up to four weeks between May and August, according to the migration timing of post-smolts which are later in the year at higher latitudes. Trawling was conducted in the outer part of the fjords to catch post-smolts migrating from all rivers within each
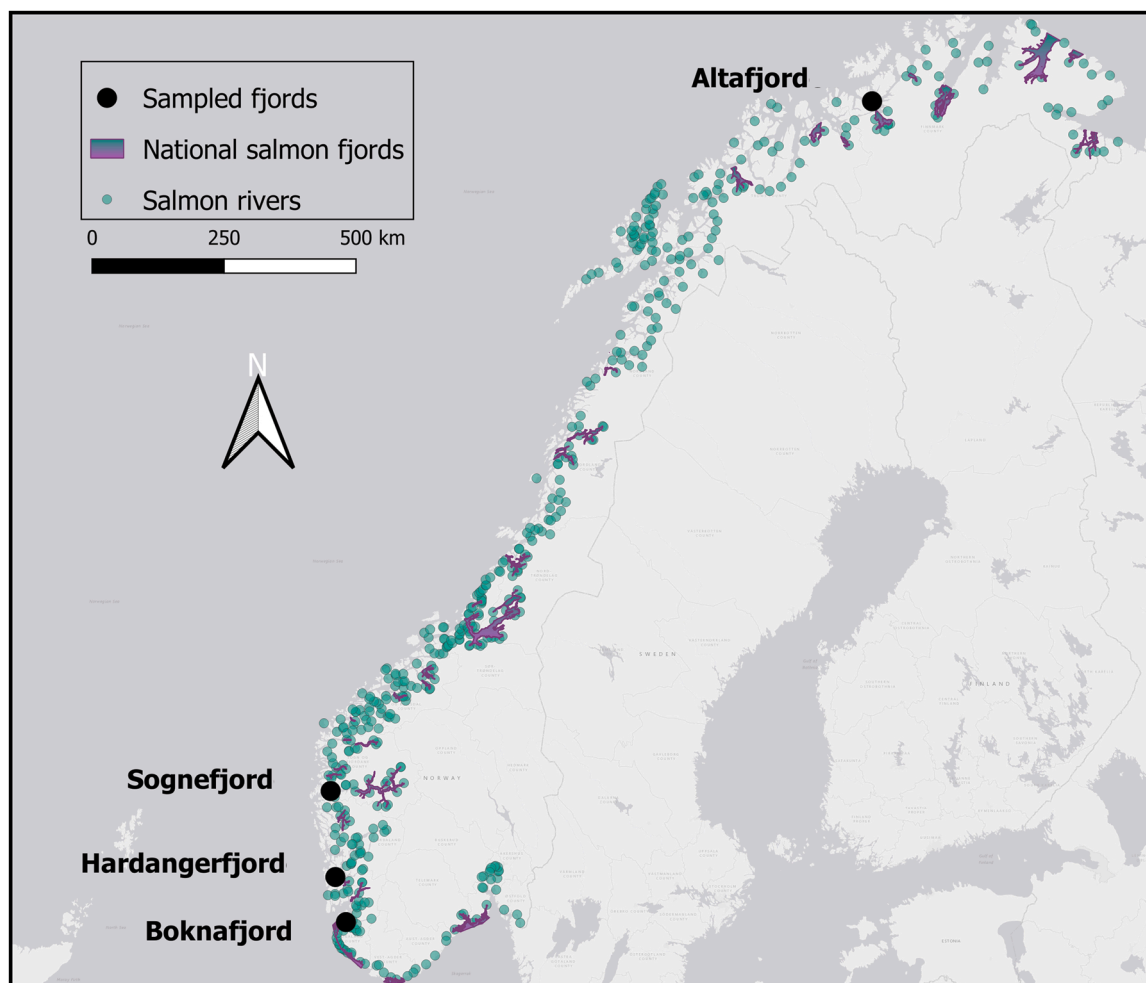

Fig. 1. Overview over Norway's coastline with salmon populations (green), national salmon fjords (purple) and sample locations (Altafjord in the north, Sognefjord, Hardangerfjord and Boknafjord in the south-west and south). Made with QGIS (QGIS Development team, 2019).

fjord, while the exact trawling transects were chosen according to the migration routes of the post-smolts, ocean currents and discharge of the rivers to optimize the probability of capturing post-smolts. Post-smolts were caught with a modified pelagic trawl that included a "FISH-LIFT" (Holst and McDonald, 2000) aquarium as a cod-end, making it possible for the fish to be kept alive after they have been caught whilst reducing physical injuries. After capture, individual post-smolts were sedated, and euthanized by a blow to the head and thereafter the wet weight (g) and body length (fork-length, mm) were measured before the fish being frozen to − 30℃ and transported to the lab in Bergen for further analysis. To compensate for shrinking observed to occur because of freezing and thawing, the body length of frozen fish were adjusted by 3% in accordance with a previous study (Rikardsen et al., 2004). A total of 578 post-smolts were used for diet analysis with similar numbers (≥ 50) per fjord and year (supplementary table 1).

2.2. Diet analysis

Post-smolt stomachs were dissected from thawed fish. Stomach content was identified to family, genus and species where possible, and thereafter, dried at 70 °C for 24 h. The dry weight to the nearest milligram was then recorded for each prey group, and a dry weight:wet weight ratio of 1:5 was applied in later calculations (Skjoldal et al., 2004). Due to low sample sizes, larval stages of euphasids (Furcilia) were grouped under Euphasiidae, other larval stages of crustaceans (Brachyura, Megalopa) were grouped as "other crustaceans" and different species of the genus Themisto (*Themisto libellula* and *Themisto abyssorum*) were furthermore described as Themisto spp. Identification of fish species was only possible for a very small number of stomachs due to advanced grade of digestion. In most cases, it could not be determined with certainty if the larvae were belonging to the group of sand eels (Ammodytes spp.), capelin (*Mallotus villosus*), or herring (*Clupea harengus*) and therefore, all fish were grouped under "Teleostei".

The following feeding indices were calculated for each fish; feeding ratio (FR) as an index of stomach fullness, Fulton's condition factor (K), frequency of occurrence (% O) which quantifies the proportion a given prey species/group found in the sampled stomach and mass percentage of prey items (% M) which quantifies mass of the prey species/group relative to other prey groups (see Table 1 for equations).

2.3. Equations and statistical analysis

General linear mixed-effects models (GLMMs) or Linear mixed effects models (LMEs) were used to investigate the multivariate relationship between post-smolt 1) feeding ratio and diet, 2) prey selectivity and post-smolt length, condition factor or diet, 3) condition factor or body length and the diet (Bates et al., 2015; Pinheiro et al., 2021). Mixed

Table 1
Equations used for data analysis.

$FR = \dfrac{100 \times m_s}{m_f - m_s}$	(1)
$K = \dfrac{m_f \times 100}{l^3}$	(2)
$\%M = \dfrac{\sum m_{s,p}}{\sum m_s} \times 100$	(3)
$\%O = \dfrac{N_p}{N} \times 100$	(4)

Where:
m_s mass of stomach content (grams)
m_f mass of post-smolt (grams)
$m_{s,p}$ mass of prey group p in the stomach content (grams)
l post-smolt body length (cm)
N_p number of post-smolt stomachs containing prey group p
N total number of post-smolt stomachs

effects models were applied to account for variation in the response variables associated with a specific fjord/year (included as random effect), but not with any of the explanatory variables and therefore of little interest for this study.

To test if stomach fullness, here expressed as feeding ratio (FR), was correlated to feeding on specific prey groups or changed with post-smolt size, the following GLMM was applied:

$$FR_i = \alpha + \mu_i + \beta_1 Tel_i + \beta_2 Eup_i + \beta_3 Amf_i + \beta_4 Cop_i + \beta_5 l_i + \beta_6 CF_i + \varepsilon_i \quad (1)$$

where *FR* is the response variable, α is the model intercept, μis a random effect for fjord and year which follow a normal distribution with mean 0 and variance σ_a^2, β_{1-6} are regression slopes, *Tel*, *Eup*, *Amf* and *Cop* (Teleostei, Euphausiids, Amphipods and Copepods) are discrete explanatory variables of whether the prey group was present in the stomach or not, *l* and *CF* are post-smolt body length and condition factor and $\mathcal{E}$ is the model residuals assumed to follow a normal distribution with expected value 0 and variance σ^2 for fish number *i*. The feeding ratio had a right-side skewed distribution and a Gamma distribution with a log-link was therefore applied in the model.

To test if the feeding behavior, which can be selective or opportunistic, varied with post-smolt size the following GLMM was applied:

$$N\_prey_i = \alpha + \mu_i + \beta_1 l_i + \beta_2 CF_i + \varepsilon_i \quad (2)$$

where *N_prey* is the number of prey groups in the stomach as an index of diet diversity. To test if post-smolts prey selectivity increases when feeding on a given prey taxa the following GLMM was applied:

$$\widehat{N\_prey}_i = \alpha + \mu_i + \beta_1 prey\_taxa_i + \varepsilon_i \quad (3)$$

The response variable $\widehat{N\_prey}$ is the number of prey types excluding the prey type being analyzed (*prey_taxa)* which is either Teleostei, Euphausiids, Amphipods or Copepods. A Poisson distribution was applied for model 2 and 3, and the final models were checked for overdispersion. Empty stomachs were excluded from the analyses with model 1 and 3, as these models test if stomach fullness (FR) and diet diversity change with diet. To include empty stomachs in such models would not be correct as any diet would lead to higher stomach fullness and diet diversity than not feeding at all.

To test if postsmolt body-length or condition factor were affected by feeding or diet, the following LME was applied with the response variables following a gaussian distribution:

$$l_i = \alpha + \mu_i + \beta_1 Tel_i + \beta_2 Eup_i + \beta_3 Amf_i + \beta_4 Cop_i + \beta_5 CF_i + \beta_6 FR_i + \varepsilon_i \quad (4)$$

$$CF_i = \alpha + \mu_i + \beta_1 Tel_i + \beta_2 Eup_i + \beta_3 Amf_i + \beta_4 Cop_i + \beta_5 l_i + \beta_6 FR_i + \varepsilon_i \quad (5)$$

Post-smolts larger than 175 mm were excluded from the analyses as larger individuals were not present in all sampled fjords. The data were inspected for outliers, collinearity, and independence prior to modeling. The parsimony principle was used to select the best model from all possible combinations of explanatory variables by selecting the model with the lowest Akaike Information Criterion (AIC) (Burnham and Anderson, 2002). For selecting the optimal LME the maximum likelihood estimator was used as the random structure was kept constant, but the final model is run with restricted maximum likelihood estimator. Homogeneity for the variance of the model residuals was checked by fitting the model residuals against fitted values and covariates. The distribution of the model residuals was also checked for normality with histograms and qq-plots.

Statistical analysis was conducted in R (R core team 2020). Packages used were ggplot2 (Wickham, 2016), dplyr (Wickham et al., 2021), gridExtra (Auguié, 2017), glmmTMB (Brooks et al., 2017) and piecewise (Lefcheck 2016).

3. Results

3.1. Overall diet composition

Of the 578 post-smolts sampled, 63 had empty stomachs. The percentage of empty stomachs was 10.4% in 2018 and 11.5% in 2019. In total, organisms from three phyla (Chordata, Arthropoda, Annelida), and five classes (Actinopterygii, Hexanauplia, Malacostraca, Insecta and Polychaeta) were found. A further five families (Calanidae, Centropagidae, Euphasiidae, Gammaridae, Hyperiidae) and nine species were identified within the prey, which included: The Copepods *Calanus finmarchicus*, *Calanus hyperboreus*, *Centropages typicus*, *Anomalocera patersoni* and *Temora longicornis*, the Amphipods *Hyperoche medusarum*, *Themisto abyssorum* and *Themisto libellula*, and the euphasid *Meganyctiphanes norvegica* (krill). Insects were often found in form of exoskeleton remains. Over 90% of the teleost prey identified within the stomachs were putatively identified as juveniles and larvae or post larvae, hereafter referred to as larvae. Across all fjords and years, the main proportion of the post-smolts' diet in mass was made up by fish larvae, krill, copepods and Themisto sp. (Hyperiidae), with 52%, 24%, 5% and 8% respectively (Fig. 2).

3.2. Spatial and annual variation between fjords

Post-smolt diet composition varied among individuals, fjords and years, but in most sampling locations several prey groups were important, both in mass percentage and frequency of occurrence (Fig. 2). Fish larvae were consumed by post-smolts from all fjords, but post-smolts from Altafjord in the north had the overall highest percentage of fish larvae (both in mass percentage and frequency of occurrence) of the four sampled fjords. In Altafjord, the percentage by weight of fish larvae decreased from 99% in 2018 to 53% in 2019, and a higher percentage of the diet was Themisto in 2019. Fish larvae were also an important food item in Boknafjord in the south, while a larger proportion of the diet were invertebrates in the two remaining fjords. In Boknafjord, the percentage by weight of fish larvae in the post-smolt diet increased from 41% in 2018 to 69% in 2019. In Sognefjord, the diet of the post-smolts changed from being dominated by insects and Themisto in 2018, to euphausiids and fish larvae in 2019. A change in the diet from 2018 to 2019 was also evident for the post-smolt sampled in Hardangerfjord, where the diet percentage by weigh increased for Euphausiids from 42% to 75% and decreased for copepods from 15% to < 1%.
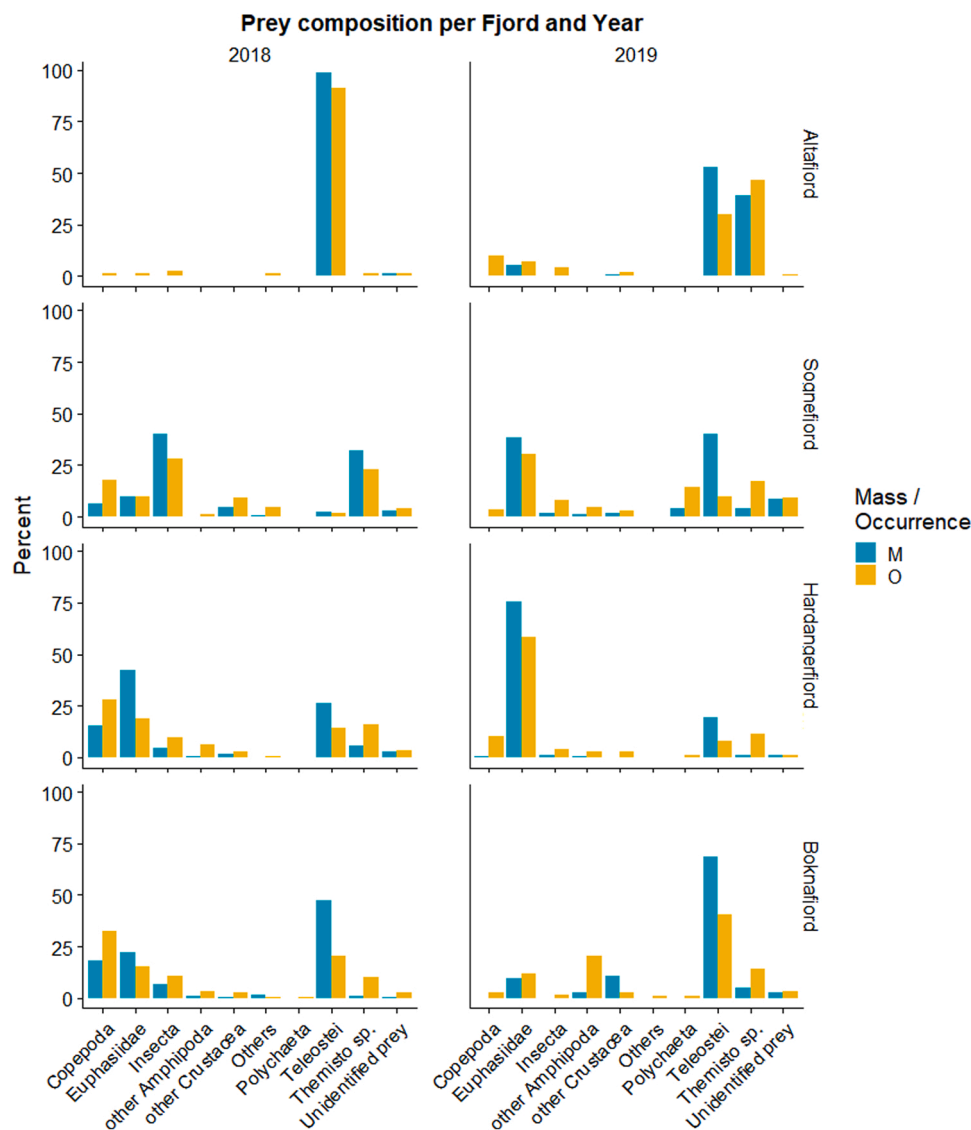

Fig. 2. Prey composition per fjord and year by mass (% M, green) and occurrence (% O, yellow).

3.3. Feeding ratio and diet diversity vary with stomach content

Across fjords and years, FR ranged from 0.001 to 5.01 for individual post-smolts. FR varied between fjords and years (Table 2, Fig. 3a). The highest average FR was found in fish from Altafjord in 2018 (1.36 ± 0.90) and lowest average FR in Sognefjord the same year (0.43 ± 0.40). Post-smolts with fish larvae or Euphausiids in their stomachs had a significantly higher FR than post-smolts without these groups, and FR decreased with post-smolt body length (Table 2, model 1). The increase in FR for post-smolts with fish larvae or Euphausiids in the stomachs changed with post-smolt body length and were on average 0.63 and 0.32 for a 14 cm post-smolt, respectively (Fig. 4). The presence of insects, copepods or Themisto in the stomachs did not have a significant effect on FR.

The number of different prey groups observed in individual post-smolt stomachs ranged from 1 to 7 different taxa. The average number of prey groups in post-smolt stomachs was lowest in Altafjord 2018 (1.1 ± 0.4), and highest in Sognefjord 2018 (3.0 ± 1.4) (Table 2, Fig. 3b). There was no effect of post-smolt body length or condition factor on the number of prey taxa found in the stomachs (model 2). Post-smolts feeding on fish larvae had fewer other prey taxa in the stomachs than post-smolts not feeding on fish larvae (Table 2, model 3). There was no difference in the number of other prey taxa found in stomachs for post-smolts feeding on Copepods or Euphausiids, while post-smolts feeding on Amphipods had a higher number of other prey taxa in the stomachs than the remaining post-smolts (Table 2, model 3).

Table 2
Estimated regression parameters, standard errors (SE) or standard deviation (SD), z- or t-values for the GLMMs or LMEs presented in Eqs. 1–5. The tested models are presented in the material and method section with model numbering, but only the tested explanatory variables which improved the model fit is presented in the table.

Variable	Estimate	S.E.	z
Response variable = FR (Feeding ratio, see Model 1)			
Fixed effect			
(Intercept)	0,7667	0,3973	1,93
Fish larvae	0,8706	0,0910	9567
Euphausiids	0,5288	0,0917	5766
Body length (cm)	-0,1091	0,0289	-3774
Random effect	SD		
Fjord&year	0,1854		
Response variable = Nprey (Diet prey diversity, see Model 3)			
Variable	Estimate	S.E.	z
Fixed effect			
Intercept	0,3035	0,2917	1041
Teleostei	-0,3490	0,0976	-3576
random effect	SD		
Fjord&year	0,8036		
Fixed effect			
Intercept	0,5463	0,0974	5607
Amphipoda	0,2405	0,1148	2094
random effect	SD		
Fjord&year	0,2550		
Response variable = Body length (cm) (see model 4)			
Variable	Estimate	S.E.	t
Fixed effect			
(Intercept)	13,5230	0,1328	101,826
Teleostei	0,5154	0,1397	3690
FR	-0,2381	0,0741	-3212
random effect	SD		
Fjord&year	0,2878		
Response variable = Condition factor (see model 5)			
Variable	Estimate	S.E.	t
Fixed effect			
(Intercept)	0,9065	0,0164	55,145
Amphipoda	0,0500	0,0170	2946
random effect	SD		
Fjord&year	0,0444		

3.4. Relationship between body length or condition factor and feeding

The average post-smolt body length per fjord and year varied between 13.1 and 14.2 cm (Fig. 3c). Post-smolts with fish larvae in the stomachs were on average 0.52 cm longer than the remaining individuals and there was a weak negative correlation between FR and body length (Fig. 4, Table 2, model 4). Feeding on amphipods, Euphausiids or copepods did not change with body length. The variation in condition factor was not explained by FR nor the presence of fish larvae, Copepods or Euphausiids in the stomachs, but the condition factor was 0.05 higher for post-smolt feeding on Amphipods (Table 2, model 5).

4. Discussion

Despite the importance of the critical life-history phase of saltwater entry and the period shortly thereafter, diet studies of Atlantic salmon post-smolts are few. In this study we were able to provide a recent dietary analysis for post-smolt captured in four Norwegian fjords nearly 20 years after the previous comparable study. The most significant results can be summarized as follows: 1. A large variation in post-smolt diet was observed among fjords and years, 2. Post-smolts that consumed fish larvae and krill displayed substantially higher feeding ratios (FR), 3. Post-smolts that consumed fish larvae did not eat many other prey taxa yet still had the highest FR.

4.1. Importance of Teleostei as a prey item

Our data indicate that the presence of Teleostei and Euphausiids in the diet greatly increases the stomach fullness of post-smolts (Fig. 4). Put simply, this suggests that access to fish larvae and large Euphausiids are important for nutrient acquisition. Marine fish larvae and crustaceans are larger and have a higher lipid content than insects that dominate the smolt diet in the freshwater phase (Rikardsen et al., 2000). In general, the results from this study confirm the results from earlier studies investigating post-smolt feeding in fjords and coastal areas, which described fish larvae as the most important prey component, but also reported Euphausiids to be important (Levings et al., 1994; Andreassen et al., 2001; Rikardsen et al., 2004; Hvidsten et al., 2009). A piscivorous diet is known to enhance growth and ultimately survival. For example, Hvidsten et al. (2009) found higher return rates of salmon in years with fish larvae as main prey for post-smolts in the fjord phase, consistent with the suggestions above. Teleostei are the only prey item where mass percentage values are higher than frequency of occurrence for all fjords in all years (Fig. 2). Even though larval stages of Euphasiidae (furcilia) were found in small numbers, both fish larvae and euphausiids were the prey groups with biggest size ingested by post-smolts. The positive correlation between stomach fullness and feeding on fish larvae and euphausiids shows that increased prey size equals higher energetic and nutritional value to the post-smolt despite the fact that such prey have longer associated handling times (Rikardsen and Dempson, 2011).

Post-smolts that had consumed fish larvae were on average 0.52 cm longer than those that had not consumed fish larvae, supporting previous findings that post-smolts need to reach a minimum size before they can effectively feed on fish larvae (e.g. Rikardsen and Dempson, 2011; Salminen et al., 2001). An alternative explanation for longer post-smolts feeding on fish larvae is that feeding on fish larvae leads to faster growth, or that fish larvae are mostly consumed in the outer parts of the fjords which most post-smolts reach after several days of feeding and growing in the sea. Although the longest post-smolts seem to have an advantage when it comes to capturing fish larvae, stomach fullness decreased with post-smolt body length (Fig. 4). A negative correlation between post-smolt stomach fullness and body length has also been reported from coastal waters outside east-USA (Renkawitz and Sheehan, 2011). We interpret this as an indication of limited prey abundance for post-smolts in the fjords in our study, assuming that the feeding efficiency is not affected by the present investigated fish sizes. The
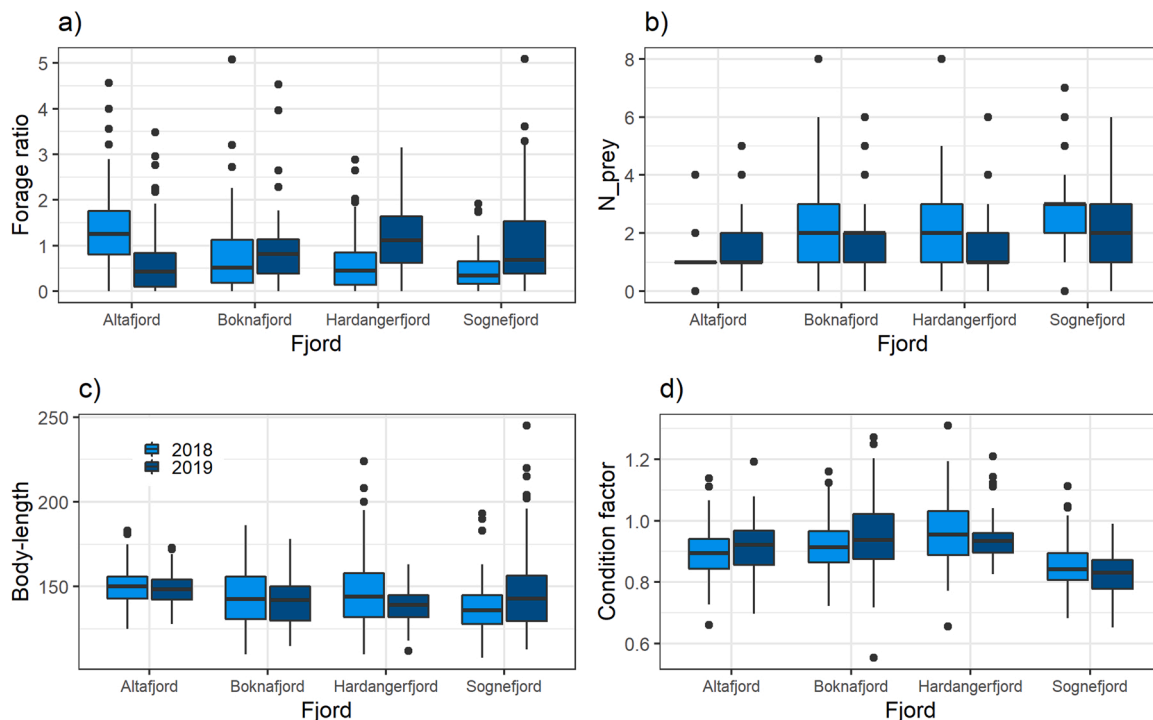
Fig. 3. Boxplots showing the observed distribution of a) Feeding ratio, b) Number of prey groups in the stomachs, c) post-smolt body length and d) Condition factor for each fjord and year of sampling.
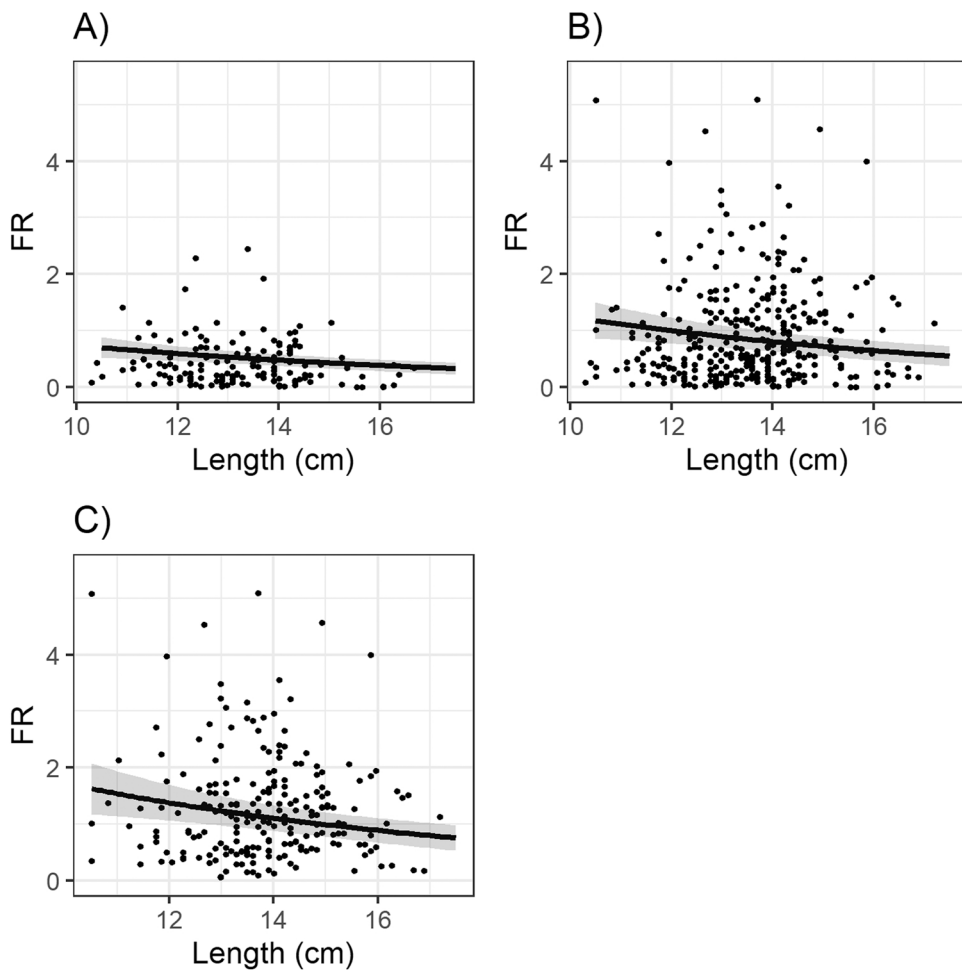

Fig. 4. Post-smolt FR as a function of body length for post-smolts A) without fish larvae or Euphausiids in the stomachs, B) with Euphausiids in the stomachs, C) with fish larvae in the stomachs. Black solid line is the estimated relationship from model (1), black dots show the data observations and gray shaded area represents the 95% confidence interval around estimated FR. Note that post-smolt consuming both fish larvae and Euphausiids are represented in Figs. 3b and 3c and the corresponding model fittings.

alternative explanation, that the longest post-smolts are too big to feed on important prey species inside the fjords, does not seem reasonable. To ensure rapid growth post-smolts must therefore migrate to better feeding grounds further offshore.

4.2. Temporal and spatial variation in post-smolt diet

Our findings showed that fish larvae dominated the diet in the northern Altafjord with entrance into the Barents Sea, while further south the diet consisted of several prey taxa and partly varied between the two years 2018 and 2019. The availability of prey items for post-smolts may vary over small distances and can therefore rapidly change as the post-smolt migrates. Therefore, part of the observed variation in post-smolt diet and stomach fullness identified in this study may reflect sampling effort varying in time and space for fjords and years. Nevertheless, our results are qualitatively similar to the results of post-smolt diet within Norwegian fjords during the 90 s and early 2000 s (Rikardsen et al., 2004; Hvidsten et al., 2009). Hence, we cannot identify any clear changes in post-smolt diet in Norwegian fjords during these nearly 20 years. Therefore, it follows that there is no clear indication of the documented Northeast Atlantic ecological regime shift affecting feeding conditions within Norwegian fjords in the time-scale of the present study. In Altafjord in the early 2000 s, post-smolt diet by weight was found to consist of 98% fish larvae and the most common species was sandeel (Rikardsen et al., 2004). In our study, the diet consisted of 99% and 53% fish larvae in 2018 and 2019, respectively. In Sognefjord, the proportion of fish larvae in the diet was 51% and 2% in 1998 and 2001 (Rikardsen et al., 2004), while in the present study it was 3% in 2018 and 41% in 2019. The proportion of crustaceans was also at the same level in 2018 and 2019 as in 1998 and 2001. No previous publications have presented data on post-smolt diet in the two remaining fjords, Boknafjord and Hardangerfjord, which represent the southernmost fjords sampled in the present study. Nevertheless, the findings presented here demonstrate that fish larvae were also important prey in this region, as this prey group for instance made up 69% of the diet by weight in Boknafjord in 2019. The average post-smolt condition factor and stomach fullness for the fish sampled in 2018 and 2019 also were within the reported range for samples from the 90ies and early 2000 s (Rikardsen et al., 2004). There was no clear indication of the Northeast Atlantic regime shift affecting post-smolt feeding conditions within fjords. This may be explained by ecosystem productivity within fjords being regulated by different circulation systems, inflow of nutrients and plankton species than further offshore (Skjoldal et al., 2004).

4.3. Niche width and prey selection

Post-smolts feeding on fish larvae had fewer other prey taxa in the stomachs than the remaining post-smolts, which indicates a selective feeding behavior, while feeding on the dominating zooplankton taxa was not associated with fewer other prey taxa in the stomachs. If we assume that fish larvae are the optimal prey for post-smolts, absence of fish larvae results in a broader diet as the post-smolt tries to cover energy requirements by preying on alternative sources of nutrients. This strongly indicates that post-smolts preferably target specific prey groups such as fish larvae when these are available, as previously reported for post-smolts in coastal waters off eastern USA (Renkawitz and Sheehan, 2011). Similar findings have been reported for post-smolts feeding in the Norwegian Sea, where a diet consisting of fish larvae and amphipods was associated with higher post-smolt stomach fullness and higher condition factor than for post-smolt having a diverse diet consisting of smaller zooplankton species (Utne et al., 2021).

If the preferred prey is not available in sufficient quantities, the alternative strategy is to target smaller prey if these are present in high abundance (Mikheev, 1984; Rincon and Lobon-Cervia, 1999; Sanchez-Hernandez and Cobo, 2015). We interpret the observed diverse diet of post-smolt without fish larvae in the stomachs to be in agreement

with this theory, where the post-smolt switch to an opportunistic feeding strategy when they do not encounter their preferred prey.

4.4. Conclusions

The findings of this study are mainly in agreement with the results of earlier studies; a large spatial and temporal variation for post-smolt stomach fullness and diet within Norwegian fjords and the importance of fish larvae as post-smolt prey. Post-smolts focus their feeding on fish larvae when encountering a high abundance of this prey group and have a diverse diet consisting of several different prey groups when fish larvae are absent. Furthermore, we found no clear evidence of changes in the post-smolt diet in recent times (2018 and 2019) compared to samples nearly 20 years earlier in the same fjords. This indicates that the ecological regime shift in the Northeast Atlantic after year 2004 did not have a large impact of post-smolt feeding conditions within Norwegian fjords, at least in the years in which samples for the present study were collected. Feeding on fish larvae did not influence condition factor. However, post-smolts sampled in this study had most likely only been in the sea for a few days, and dietary differences may therefore only have had a minor effect on energetic state in this short period.

CRediT authorship contribution statement

Lea Marie Hellenbrecht: Methodology, Investigation, Formal analysis, Writing – original draft. **Kjell Rong Utne**: Conceptualization, Formal analysis, Supervision, Writing – original draft, Writing – review & editing. **Ørjan Karlsen**: Project administration, Conceptualization, Writing – review & editing. **Kevin Alan Glover**: Conceptualization, Supervision, Writing – original draft, Writing – review & editing. **Vidar Wennevik**: Methodology, Conceptualization, Supervision, Writing – review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.fishres.2023.106672.

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